Monophyly of the dacetonine tribe-group and its component tribes (Hymenoptera: Formicidae)

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SYNOPSIS. Within the large subfamily Myrmicinae three independent tribes of ants, Basicerotini, Dacetonini and Phalacromyrmecini, are each recognised as monophyletic and are shown together to constitute a monophyletic tribe-group, here termed the dacetonine-group. Synapomorphies uniting the tribe-group and autapomorphies isolating each tribe are identified and discussed; comments on potential synapomorphies among the three tribes are given.

INTRODUCTION

For many years it has been obvious that the classification of the ant subfamily Myrmicinae at tribe rank is inadequate, with genera or groups of genera being associated on flimsy evidence or merely on superficial similarity. The most recent synoptic classifications (Hölldobler & Wilson, 1990; Bolton, 1994) only serve to stress the rather decrepit nature of the structure. Detailed analysis of the subfamily to produce an accurate higher classification at this rank is in its infancy. Past work on myrmicine larvae (G. C. Wheeler & J. Wheeler, 1976) and sting structure (Kugler, 1979) has

done little to clarify the overall position, although the latter does indicate a number of potentially interesting groupings. An investigation of myrmicine comparative morphology which is currently taking place is unearthing many characters of value in establishing a natural tribe-rank classification. The aim of this paper is to establish, through morphological characters, the monophyly of three tribes within the Myrmicinae, namely Basicerotini, Dacetonini and Phalacromyrmecini, and to show that the three together form a monophyletic group.

Most members of all three tribes nest and forage in leaf litter, topsoil or rotten wood where they form small, usually monogynous, colonies. Only few for-

age openly on the surface of the ground and few are arboreal or occur very deep in the soil. All known species are predatory, mainly catching entomobryomorph Collembola but with numerous species also preying on a wide range of other small arthropods such as sminthurid Collembola, Diplura, Symphyla, Chilopoda, Pseudoscorpiones, Acarina, Araneae, Isopoda, Amphipoda, and many orders of small Insecta and their larvae (Wilson, 1953, 1956; Carlin, 1982; Masuko, 1985; Wilson & Brown, 1985; Dejean, 1987a, 1987b and included references). Species and individuals are common in Berlese or Winkler bag samples of leaf litter or rotten wood throughout the tropics. They may be numerous or locally abundant (e.g. Belshaw & Bolton, 1994; Fisher, in press).

Dacetonini is a large tribe with a world wide distribution. At the last count it included 395 described species (Bolton, 1995a) but many more species have been diagnosed since and their taxonomy is currently being studied by the author. The vast majority of dacetonine species are tropical or subtropical but the tribe is also well represented in zones with a mediterranean climate. Some species occur endemically as far north as Switzerland and Georgia in the West Palaearctic (Kutter, 1977; Arakelian & Dlussky, 1991), and Japan in the East Palaearctic (Morisita, Kubota, et al., 1992). In North America one species ranges as far north as the USA – Canada border (Brown, 1953a). In the southern hemisphere dacetonine species occur as far south as New Zealand (Brown, 1953b), the southernmost parts of South Africa (Bolton, 1983), and central Argentina (Brown, 1962).

Basicerotini mostly shows a Gondwanic distribution, with many species occurring in the Neotropical and Australasian regions (Brown & Kempf, 1960). In the New World basicerotines have been recorded as far north as Florida in the USA (Deyrup, Johnson, et al., 1989) and as far south as Argentina (Kempf, 1972). The tribe is also well represented in Indonesia, Malaysia, the Philippines and the Pacific islands (Taylor, 1990) but is absent from the Holarctic, Afrotropical, Malagasy and Oriental regions. Currently there are 64 described species (Bolton, 1995a), but more await description in various collections.

Phalacromyrmecini is a widely distributed but small and apparently relict tribe that contains only 3 described species (Bolton, 1984), each comprising a monotypic genus. Two of these have only been collected once. They have been found in Brazil, Madagascar and Malaysia.

The three tribes together thus have 462 described species, representing over 10% of the subfamily Myrmicinae, itself easily the largest subfamily in the family Formicidae. The Myrmicinae, which contains 4377 species, represents over half the total described for the entire family. The monophyly of Myrmicinae is probably certain and is documented elsewhere (Baroni Urbani, Bolton & Ward, 1992). Bolton (1994) gives a modern definition of the subfamily and keys to its genera, and all its species are catalogued in Bolton (1995b).

TAXONOMIC HISTORY

Dacetonini is the oldest suprageneric name in the group, initiated by Forel (1892) to include the genera (in the order that he gave them) Strumigenys, Orectognathus, Epitritus, Hypopomyrmex [a fossil taxon], Daceton, Acanthognathus, Rhopalothrix, Ceratobasis [now a synonym of Basiceros] and Cataulacus. By modern reckoning this is a fairly disparate group and Forel gave no definitive diagnosis. The next year Forel (1893) listed these same genera, as Myrmicinae tribe Dacetonii, in a synoptic classification. Emery (1895) also produced a synopsis in which he rendered the tribe name as Dacetii. He did not mention the fossil Hypopomyrmex and rightly excluded Cataulacus from the tribe. The first formal diagnosis of Dacetonini was produced in key form by Emery (1896) with the above inclusions and exclusions. The tribe remained stable with these seven genera for a number of years (W. M. Wheeler, 1910).

In later synopses and classifications other genera, described in the intervening years and referred to Dacetonini, were added, for instance Stegomyrmex, Microdaceton, Pentastruma by the time of Emery (1914), who spelled the tribe name as Dacetini; Glamyromyrmex and Epopostruma by the time of Forel (1917); Blepharidatta by the time of Emery (1922); Codiomyrmex by the time of W. M. Wheeler (1922), who also correctly excluded Stegomyrmex and Blepharidatta.

Over the twenty years that followed this a number of authors added further genera to the tribe, until by 1945 the number of genera stood at about 21. Shortly afterwards Brown (1948) began a series of revisionary studies on the generic composition of the tribe, adding a number of new genera. Subsequent papers (Brown, 1949a, 1949b, 1949c, 1950a, 1950b, 1952, 1953a, 1954) refined his concept of the tribe and its component genera. Several more new genera were described, some were synonymised, a number of incorrectly placed taxa were excluded, and the ranks of several genus-group taxa were adjusted. The tribe was subdivided into five subtribes (Brown, 1952) and a proposed evolutionary sequence within the tribe was produced (Brown & Wilson, 1959). A very old name, the fossil Hypopomyrmex that had been one of the original members of the tribe (and sole member of subtribe Hypopomyrmiciti), was finally reassesed (Brown & Carpenter, 1979) and decisively excluded.

In one paper of his revisionary series Brown (1949c) recognised that a number of closely related genera

formed a uniform group that could be excluded from Dacetonini. These genera (*Acanthidris, Basiceros, Creightonidris, Heptastruma, Octostruma, Rhopalothrix* and *Talaridris* in the 1949 paper) were grouped together as the tribe Basicerotini. The species of all these were later fully revised on a world basis by Brown & Kempf (1960).

At about the same time Kempf (1960) described an oddly dacetonine-like genus (*Phalacromyrmex*) which together with two other small genera was diagnosed as a discrete genus group by Bolton (1984). A tribe rank name, Phalacromyrmecini, was applied to this group by Dlussky & Fedoseeva (1988), citing the Bolton (1984) definition. [Earlier uses of the name Phalacromyrmecini by G. C. Wheeler & J. Wheeler (1976, 1985) are unavailable as they do not satisfy Article 13 (a) of the International Code of Zoological Nomenclature, third edition, 1985.]

Thus by the early 1990s the classification and generic content of the three tribes had reached the state outlined below, full references for which can be obtained from Bolton (1995b). The synopsis given here indicates all names in the genus group that are currently included in the three tribes. The names listed in parentheses are current junior synonyms. Figures in square brackets after the tribe names indicate the number of species examined for characters visible without dissection; a list of species dissected is appended below.

Tribe **Dacetonini** [569]

Subtribe Dacetoniti [5]
    Genera: *Acanthognathus, Daceton (=Dacetum).*
Subtribe Epopostrumiti [15]
    Genera: *Colobostruma (=Alistruma, =Clarkistruma), Epopostruma (=Hexadaceton), Mesostruma, Microdaceton.*
Subtribe Orectognathiti [14]
    Genus: *Orectognathus (=Arnoldidris).*
Subtribe Strumigenyiti [535]
    Genera: *Asketogenys, Chelystruma, Cladarogenys, Codiomyrmex, Codioxenus, Dorisidris, Dysedrognathus, Epitritus, Glamyromyrmex (=Borgmeierita), Gymnomyrmex, Kyidris (=Polyhomoa), Neostruma, Pentastruma, Quadristruma, Serrastruma, Smithistruma (=Cephaloxys, =Miccostruma, =Platystruma, =Weberistruma, =Wessonistruma), Strumigenys (=Eneria, =Labidogenys, =Proscopomyrmex, =Pyramica), Tingimyrmex, Trichoscapa.*

Tribe **Basicerotini** [49]

    Genera: *Basiceros (=Ceratobasis, =Aspididris), Creightonidris, Eurhopalothrix, Octostruma, Protalaridris, Rhopalothrix (=Acanthidris, =Heptastruma), Talaridris.*

Tribe **Phalacromyrmecini** [3]

    Genera: *Ishakidris, Phalacromyrmex, Pilotrochus.*

Until 1994 characters defining the tribes tended to be of an inclusive nature. They were organised in such a way that all taxa showing a particular combination of characters were included in the tribe, those not showing such a combination were excluded. Usually none of these characters could be obviously pointed out as apomorphic. Along these lines the most recent inclusive definitions of the tribes were Brown (1953a) for Dacetonini, Brown & Kempf (1960) for Basicerotini and Bolton (1984) for Phalacromyrmecini.

Baroni Urbani & de Andrade (1994) identified the first synapomorphy exhibited by, and thus unifying, all three tribes: opposing, as distinct from overlapping, mandibles. They also demonstrated that some characters regarded in the past as potential synapomorphies (head shape, specialised hairs) had no real value. Failing to find apomorphies for the individual tribes within the bounds of their synapomorphy, they terminated the independent existence of Basicerotini and Phalacromyrmecini, treating them as junior synonyms of Dacetonini. Although the Baroni Urbani & de Andrade (1994) position was summarily reversed in Bolton's (1995b) catalogue, their approach provided a useful starting point for a detailed investigation. Based on the result of their work, the hypothesis postulated was that only a single real tribe is represented. Characters were then sought and analysed to validate or disprove the results of that assumption. The results obtained indicate that the hypothesis is incorrect and that three tribes should be recognised. The diagnosis and discussion of the relevant characters follows this section.

The present investigation is based upon the worker caste, although most if not all of the characters mentioned are also applicable to known queens. Males are excluded from the survey for the simple reason that they remain utterly unknown in phalacromyrmecines and in several genera of the other tribes. Even in the larger genera males are only very scantily represented. This means that selection of universal characters cannot even be implied, let alone be guaranteed. For the sake of this paper each currently recognised genus in the classification outlined above is assumed to be a valid taxon at genus rank, although work in progress indicates that many should not have such status.

MONOPHYLY OF THE DACETONINE TRIBE-GROUP

The tribes Basicerotini plus Dacetonini plus Phalacromyrmecini share five worker/queen synapo-

morphies and therefore together form a monophyletic group within the subfamily Myrmicinae. The synapomorphies are listed and discussed below, each under its own heading. Character polarity here and in subsequent sections is determined by comparison with those groups currently recognised as the most morphologically generalised Myrmicinae (Myrmicini, Tetramoriini, Formicoxenini). Characters and states across the entire subfamily have been taken into consideration to account for cases of convergence.

Synapomorphies of the dacetonine tribe-group

Masticatory margins of mandibles oppose but do not overlap at full closure
Throughout the three tribes the masticatory (inner) margins of the mandibles fail to overlap or cross over when the mandibles are fully closed. In taxa with serially dentate mandibles the main dental rows interlock tightly at full closure (Figs. 5, 10, 15, 23) rather than the dental row on one mandible passing over the other (Figs. 1, 2, 4), although a few teeth at the extreme apices may cross over (Figs. 11, 22). In taxa with elongate or linear mandibles the inner margins oppose each other, or touch for part of their length at full closure, but do not overlap (Figs. 13, 14, 24). In such forms where a long preapical spiniform tooth occurs, or where an apical fork of spiniform teeth is developed, the teeth themselves may interlock or cross, but the margins from which they arise do not do so (Figs. 13, 14, 33).

This is the character first recorded by Baroni Urbani & de Andrade (1994) and is apomorphic through the groups under consideration. With one exception other Myrmicinae, including all the tribes regarded as morphologically most generalised on other grounds (Myrmicini, Tetramoriini, Pheidolini, Formicoxenini), have the mandibles plesiomorphically overlapping at full closure (Figs. 1, 2, 4). The exception is the peculiar monotypic genus *Tatuidris* (Fig. 6), the sole extant member of tribe Agroecomyrmecini, which also has opposing mandibles. That this is a non-homologous parallelism with the dacetonine-group is easily demonstrated.

Tatuidris has the following apomorphies; the corresponding plesiomorphies exhibited throughout the dacetonine-group are given in square brackets.

1. Tergite and sternite of first gastral segment (abdominal segment 4) are fused. [First gastral tergite and sternite unfused.]
2. First gastral sternite reduced, very much shorter than tergite, so that first gastral segment is directed ventrally with respect to the postpetiole. [First gastral sternite full-sized; first gastral segment not directed ventrally.]

3. Mandible with a thick brush of stout setae on inner surface. [Mandible without setal brush.]
4. Eyes at extreme posterior apex of scrobe. [Eyes not at posterior apex of scrobe.]
5. Antennal sockets extremely widely separated. [Antennal sockets relatively close together.]
6. Alitrunk very short and compact, in profile higher than long. [Alitrunk elongate; in profile usually longer than high.]
7. Apicotibial brush of thick dense setae present on foretibia opposite strigil. [Apicotibial brush absent.]

Conversely *Tatuidris*, beside lacking other dacetonine-group apomorphies, has the following characters exhibiting plesiomorphic states; their corresponding apomorphic expressions in the dacetonine-group (and mostly elsewhere in the Myrmicinae) are in square brackets.

1. Postpetiole very large, very broadly articulated to gaster. [Postpetiole small and narrowly articulated to gaster.]
2. Sternite of postpetiole large, in profile almost as extensive as tergite. [Sternite of postpetiole reduced, much smaller than tergite.]
3. Petiole sessile. [Petiole pedunculate.]
4. Tibial spurs pectinate, strongly developed on middle and hind legs. [Tibial spurs not pectinate, vestigial to absent on middle and hind legs.]

Anterior head capsule is narrowed from side to side
In the three dacetonine-group tribes the head in full-face view, anterior to the antennal sockets, is relatively narrow. A line drawn parallel to the long axis of the head, touching the outermost point of the torulus, will pass outside or very close to the point where the outer margin of the fully closed mandible intersects the anterior clypeal margin (Figs. 5, 7, 10, 13, 14, 15, 22, 23, 24, 33). In all other Myrmicinae (except for the few with radically migrated toruli discussed below) a line so constructed will pass considerably mesad of the point where the outer margin of the fully closed mandible intersects the anterior clypeal margin (Fig. 1).

The anterior narrowing of the head can be expressed as a ratio, the Mandibular-Torular Index (MTI), which with the head in full-face view may be defined as: distance between points where outer margins of fully closed mandibles intersect anterior clypeal margin *divided by* distance between outermost points of lower margins of toruli. Thus when MTI = 1.0 the two measurements are equal. MTI range of 0.5–1.3 is shown by the dacetonine-group of tribes, and also by *Tatuidris* (Fig. 6), *Cataulacus* (Fig. 4) and some Cephalotini. Other tribes of Myrmicinae together have MTI range 1.5–>3.0. The reason why these three non-dacetonine taxa have a similar MTI range to the dacetonine-group

is that whilst their heads have remained plesiomorphically broad anteriorly, their toruli have secondarily migrated outwards on the cephalic dorsum, bringing them into line with the clypeal intersection points of the mandibles. Thus two completely different evolutionary routes, static toruli combined with narrowed anterior head (the dacetonine-group), *versus* static broad anterior head combined with outwardly migrated toruli (*Tatuidris, Cataulacus,* some Cephalotini), will give the same overall MTI result. For an illustration of this character spanning the entire subfamily compare the full-face view photographs of the various myrmicine genera in Bolton (1994).

As a direct result of the narrowing of the anterior head the dacetonine-group shows a number of other derived characters that are unavoidable corollaries of this modification.

1. Width of labrum at base, and consequently also of clypeo-labral hinge, is reduced (see below).
2. Width of buccal cavity, and consequently also of labio-maxillary complex, is reduced (compare Fig. 3 with Figs. 12, 26, 28).
3. Anterolateral surface of head tends to be vertical, or nearly so, and is very close to or more or less directly below the antennal socket (e.g. Figs. 11, 18, 19, 32).

Preocular carina is present
With the head in profile or dorsolateral view there is a ridge, carina or lamella that originates at the posterolateral termination of the clypeus, extends posteriorly below the antennal socket and usually continues for some distance towards the level of the eye (Figs. 11, 18, 19, 30, 32). In many taxa this preocular carina is also visible in full-face view, at least anteriorly (Figs. 13, 23, 25, 31), but usually cannot be seen in this view in those species or genera where the frontal lobes and frontal carinae are strongly expanded laterally (Fig. 7).

Morphologically the carina represents the exaggerated outer margin of the antennal fossa and is another corollary of the narrowing of the head (particularly of number 3, immediately above). At its weakest the carina is a ridge that emphasises the dorsalmost line of the more or less vertical side of the head capsule. At its strongest it is a broad, laterally projecting lamella. The structure is perhaps better termed the subtorular carina or subantennal carina as this area is always where it is strongest developed, but earlier literature has used preocular carina so much that the name will probably be retained.

Specialised range-finder/trigger hairs are developed on the mouthparts
In the dacetonine-group hunting always seems to involve an open-mandible approach to the prey, followed

by a rapid strike with the mandibles (see references above, particularly Masuko, 1985). The strike may be followed by static pressure of the mandibles, merely to retain a grip on the prey until the sting can be brought into use ('strike-hold-sting' technique), or dissipation of the kinetic energy of the strike itself may be sufficient to shock the prey into immobility, even if only temporary, until the sting can be brought into play, particularly if the prey is lifted clear of the ground immediately after the strike ('strike-lift-sting' technique). Whatever the technique, the explosive closing of the mandibles is initiated by activation of a trigger which consists of one or more specialised hairs on the mouthparts. Contact with prey by these hairs commences a sequence of events that causes the mandibles to snap shut (Masuko, 1985; Gronenberg, 1996). In the vast majority of dacetonine-group taxa these hairs arise from the anterior margin of the labrum or the apices of the labral lobes (Figs. 16, 25–31 (broken off short in 26), 27, 33), more rarely from the mandible itself; such trigger hairs are not found elsewhere in the Myrmicinae.

Specialisation of the labrum
Except for the dacetonine-group of tribes the structure of the labrum is very uniform and generalised in the Myrmicinae (Gotwald, 1969 and present investigation), and this same structure is prevelent throughout the Formicidae. Outside the dacetonine-group the labrum is a simple sclerite (Fig. 3) that is broader than long and broadly hinged to the clypeus. Its posterior margin, which is attached to the clypeus, is more or less straight. Its anterior (free) margin is indented or cleft medially so that in general the labrum appears broadly B-shaped, or D-shaped with a median indentation in the anterior free margin. The clypeo-labral hinge is mobile so that at rest the labrum folds back and down with respect to the clypeus. In this position it tightly overlaps and protects the delicate apical portions of the labio-maxillary complex. In the Myrmicinae this is the plesiomorphic shape and position. It is encountered in all the morphologically more generalised tribes (e.g. Myrmicini, Tetramoriini, Pheidolini, Pheidologetonini, Formicoxenini, Solenopsidini), as well as in those that are rather more specialised morphologically (e.g. Attini, Cataulacini, Cephalotini, Crematogastrini, Stenammini, Agroecomyrmecini).

Tribes in the dacetonine-group show a number of modifications away from the generalised structure illustrated in Fig. 3, but all are based on labral narrowing and elongation, and loss of the basic broadly B- or D-shaped outline.

In taxa with mandibles that use static pressure, regardless of whether the mandibles are long or short, the labrum becomes longer and narrower, sometimes longer than broad. The sclerite usually terminates in

one or two exaggerated anterior lobes or linguiform prominences that bear the trigger hairs (Figs. 12, 16, 25, 28, 29, 31). In these forms the labrum can usually still flex down very slightly, but it is not capable of tight closure against the labio-maxillary complex (Figs. 12, 28). Conversely, in some taxa the labrum is hyper-trophied and elongate-linguiform; instead of concealing only the apex of the labio-maxillary complex it covers the entire buccal cavity (Fig. 32). Taxa with long kinetic mandibles tend to have the labrum very narrow basally, and more distally to develop a pair of laterally projecting processes or arms; the sclerite therefore tends to be roughly T-shaped and its apex functions to prop open the mandibles prior to striking (Figs. 26, 27, 30). One long-mandibulate genus (*Acanthognathus*) has eliminated the labrum from this function and here it is represented only by a very slender, inverted Y-shaped sclerite.

Some characters considered but not used at tribe-group rank

Presence of 2-segmented antennal club
An antennal club of two segments is universal in the tribes Basicerotini, Dacetonini and Phala-cromyrmecini, though only very poorly expressed in *Daceton*. This may be the result of a single evolution-ary event in the dacetonine-group, but a two-segmented club is also developed in a wide range of non-dacetonine myrmicine taxa. For example, a strongly defined two-segmented club is universal in Melissotarsini (*Melissotarsus, Rhopalomastix*), present in all the core genera of Pheidologetonini (*Afroxyidris, Carebara, Oligomyrmex, Paedalgus, Pheidologeton*), present in some but by no means all Stenammini (*Adelomyrmex, Baracidris, Lachnomyrmex, Mayriella, Tetheamyrma*), occurs in a few Solenopsidini (*Carebarella, Solenopsis*) and is present in the single extant genus of Agroecomyrmecini (*Tatuidris*). It is weakly developed in some Blepharidattini (*Blepharidatta, Wasmannia*), and in some but not all species of *Cardiocondyla* (Formicoxenini) and *Crematogaster* (Crematogastrini).

Antennomere count
Although very useful as a character in keys, antennomere count was ignored in this survey because in some myrmicines there is variation within genera (e.g. 10, 11 or 12 in *Tetramorium* (Tetramoriini); 4, 5 or 6 in *Smithistruma* (Dacetonini)). Also, within the tribes of the dacetonine-group there is a wide range of counts that makes analysis very difficult. For example in Dacetonini counts of 4, 5, 6 and 11 have been recorded; in Basicerotini 7, 8, 9 and 12, and in Phalacromyrmecini 8, 9 and 11. I am convinced that these counts indicate independent morphoclinal reductions within each tribe, with no significance at tribe rank.

Absence of tibial spurs
Throughout the tribes of the dacetonine-group spurs are absent from the middle and hind tibiae. This condi-tion is apomorphic among the Myrmicinae but unfortunately is so extremely widespread through the subfamily that it has very little analytical value in the current survey.

MONOPHYLY OF TRIBE BASICEROTINI

Basicerotini Brown

Basicerotini Brown, 1949c: 86. Type-genus: *Basiceros* Schulz, 1906: 156. [Basicerotini relegated as junior synonym of Dacetonini by Baroni Urbani & de Andrade, 1994: 10; revived from synonymy by Bolton, 1995b: 9.]

Apomorphies of tribe Basicerotini

Each worker apomorphy is briefly described, in some cases with added comments where unrelated taxa show similar but non-homologous modifications. The plesiomorphic state of each character is given in square brackets; in some cases alternative apomorphic condi-tions are also noted for comparative purposes.

LABRUM
Distal of the hinge with the clypeus the labrum has a deeply incised transverse groove or trench across its entire dorsal width. The distal margin of this groove is defined by a sharp edge, ridge or crest (Fig. 16; also visible between the closed mandibles in Figs. 13, 14). [Labrum without sharply defined transverse groove distal of hinge.]

   In the basicerotines this groove, or at least its sharp distal margin, is usually located far enough anteriorly on the labrum as to be visible in ordinarily mounted specimens which have the mandibles ajar and the labrum slightly depressed.

TORULUS
The dorsal lobe of the torulus is hypertrophied and strongly curved downwards (Figs. 18, 19); its outer surface is nearly vertical so that it conceals part to most of the condylar bulb of the scape and the antennal socket itself. [Torulus a simple annulus or with a small lobe present dorsally that is horizontal and does not conceal the condylar bulb of the scape and the antennal socket.]

SCAPE NECK ARTICULATION
Because of the size and shape of the torulus the space in which the basal neck of the scape (the short narrow section between condylar bulb and scape shaft proper)

can move is narrow and directed fore and aft (Figs. 18, 19). [Space in which basal neck of scape can move is not restricted to a narrow fore and aft motion.]

BASE OF SCAPE
Scape shaft near base is bent downwards through a right-angle or near right-angle; the articulatory condyle at the extreme base projects forward from this through another right-angle that is not in the same plane as the first bend but rather is rotated through about 90 degrees (Figs. 8, 9). [Scape shaft in a straight line with basal condyle; or if scape angled downward near base then angle of basal condyle remains in the same plane as the shaft and is not rotated through 90 degrees.]

ANTENNAL FOSSA
Antennal fossa separated from scrobe by at least a cuticular rim or crest; the depressed fossal area surrounded on all sides by raised or prominent cuticle (Figs. 18, 19). [Antennal fossa and scrobe confluent (when the latter is developed).]

SCROBE
Scrobe always present and located below the eye (Figs. 18, 19), the latter usually situated on the extreme dorsolateral rim of the scrobe, more rarely towards underside of upper scrobe rim (very rarely eye absent). [Scrobe absent, or present but extending above the eye (eye sometimes absent).]

Some other myrmicine taxa have a scrobe that extends below the eye, namely *Cataulacus*, some Cephalotini, and the Dacetonini related to *Epopostruma* (Epopostrumiti in the synoptic classification above). *Cataulacus* and the few cephalotines with this condition can be dismissed as obvious convergence. Not only is the basic structure of the scrobe dissimilar but also the detailed structure of the head is very different. They lack, of course, the apomorphies of the dacetonine-group of tribes and exhibit their own series of apomorphies. The Epopostrumiti, on the other hand, belong in the dacetonine-group. Apart from possessing the apomorphies of Dacetonini and lacking those of Basicerotini, the scrobes in Epopostrumiti lack sharply defined posterior margins, usually lack ventrolateral margins and, except in a very few species, fail to extend forward to the mandibular articulation (Fig. 32); all of these are developed in Basicerotini. Finally, a morphocline of species in the genera *Colobostruma* – *Mesostruma* – *Epopostruma* is present that exhibits a gradual increase in development and definition of the scrobe; no basicerotine could be inserted into the series, nor added to either end.

OCCIPITAL FORAMEN
The occipital foramen is set in a deep depression on the occipital surface of the head; cuticular margination is continuous around the depressed area (Fig. 17). [Occipital foramen not set in a continuously marginate deep depression.]

A very few Dacetonini have a transverse ventral rim of cuticle below the occipital foramen. This structure is very different from the basicerotine organisation.

HELCIUM
Helcium arises from the base of a broad, deeply concave depression or excavation in the anterior surface of the postpetiole (Fig. 20). [Helcium not set in a concave depression.]

GASTER
First gastral tergite and sternite each distinctly transversely marginate basally, immediately behind the postpetiole (Fig. 21). [First gastral tergite and sternite not marginate basally.]

Members of the strumigenyite group of Dacetonini genera have a specialised transverse crest on the first gastral tergite, the limbus, which is an apomorphy of that group. The limbus is located prebasally and is inclined towards the base proper, where it overhangs the presclerites of the segment. It is not a homologue of the basal margination developed in Basicerotini. No Dacetonini have a basally marginate first gastral sternite.

SCULPTURE
First gastral tergite and sternite with characteristic sculpture of dense, sharply incised, separated punctures (e.g. Fig. 21). [First gastral tergite and sternite unsculptured, or with different sculpture.]

This character may seem rather imprecise, but the form of sculpture is striking and not obviously repeated elsewhere. A very few individual basicerotine species have secondarily reduced or effaced the sculpture. Elsewhere in the dacetonine-group, and in the Myrmicinae as a whole, are many species with sculptured gasters. Even when the sculpture in these is of a basically punctate form it tends to be reticulate-punctate or sparse, or on one sclerite but not the other. It is not the dense deeply-incised punctation exhibited by the Basicerotini on both sclerites.

MONOPHYLY OF TRIBE DACETONINI

Dacetonini Forel

Dacetonini Forel, 1892: 344. Type-genus: *Daceton* Perty, 1833: 136.

Apomorphies of tribe Dacetonini

The two worker apomorphies are briefly described and comments added. The plesiomorphic state of each character is given in square brackets.

MANDIBLE
Mandible with a medially projecting cuticular process present on the inner margin close to the base

(basimandibular process); the process not merely a modified tooth (Figs. 25, 26, 27, 31, 33). [Mandible without a basimandibular process.]

In some dacetonine taxa the basimandibular process is visible in ventral view in ordinarily mounted specimens, but in most the mandibles need to be opened quite widely or the labrum depressed. The process is variably shaped in different dacetonine taxa, taking the form of a lobe, a short or long spur, or a lamella (basal lamella). In all dacetonines except *Acanthognathus* the basimandibular process inserts between the clypeus (above) and the labrum (below) when the mandibles are closed and is part of the jaw locking mechanism. In *Acanthognathus* the process is hypertrophied but passes ventral to the labrum as the latter is vestial in this genus and no longer serves in the jaw locking mechanism.

A few basicerotine species in the genera *Eurhopalothrix* and *Octostruma* have the basal tooth of the mandible flattened or lengthened. This is not homologous with the dacetonine basimandibular process, which is derived from the mandible itself and not from a tooth. Basicerotine species with a modified basal tooth are exceptional and certainly best regarded as independent acquisitions. The usual condition is to have the basal tooth quite normal; presence/absence of a flattened basal tooth cannot be used diagnostically either at genus or species-group rank.

LABRUM
Dorsal surface of labrum with an impression or pair of impressions located medially on the labral shield, distal of the basal hinge but proximal of the labral lobes (Figs. 27, 30). [Labrum without mid-dorsal impression.]

The labral impression receives the basimandibular processes of the mandibles when they are fully closed. The character is not repeated anywhere else in the Myrmicinae. It is secondarily lost in *Acanthognathus* because, as pointed out above, the labrum is secondarily extremely reduced in this genus.

MONOPHYLY OF TRIBE PHALACROMYRMECINI

Phalacromyrmecini Dlussky & Fedoseeva

Phalacromyrmecini Dlussky & Fedoseeva, 1988: 80 [based on diagnosis in Bolton, 1984: 381]. Type-genus: *Phalacromyrmex* Kempf, 1960: 89. [Phalacromyrmecini relegated as junior synonym of Dacetonini by Baroni Urbani & de Andrade, 1994: 10; revived from synonymy by Bolton, 1995b: 9.]

Apomorphies of tribe Phalacromyrmecini

Each worker apomorphy is briefly described and comments added. The plesiomorphic state of each character is given in square brackets.

MANDIBLE
Dentition of alternating large and small teeth from base to apex; largest tooth usually the basal. [Dentition not of alternating large and small teeth; largest tooth usually the apical.]

A few isolated species or small species-groups in the dacetonine genus *Glamyromyrmex* have the basal tooth the largest on the masticatory margin, but these lack alternating dentition.

MESOPLEURON
Katepisternum with an impression or groove extending obliquely downward from posterior margin of mesopleural hair-filled gland towards metapleuron; impressed area usually bounded by ridges or carinae. [Katepisternal oblique groove absent.]

SCAPE
Scape slender basally, clavate apically; entire scape roughly Indian-club shaped. [Scape subcylindrical.]

POTENTIAL SYNAPOMORPHIES BETWEEN PAIRS OF COMPONENT TRIBES

The object of this paper has been to establish the monophyly of the tribes and the tribe-group, rather than to produce a formal phylogeny. However, a number synapomorphies potentially linking pairs of tribes within the group have been noticed and these are mentioned below. The plesiomorphic state expressed by the isolated tribe in each set is given in square brackets.

Potential synapomorphies of Dacetonini + Phalacromyrmecini

POSTPETIOLE-GASTER ARTICULATION
Diameter of presclerites of abdominal segment 4 (=first gastral segment) small and constricted so that the postpetiole-gaster articulation is relatively narrow. [Basicerotini: diameter of these presclerites broad so that the postpetiole-gaster articulation is relatively wide.]

PRESCLERITE OF FOURTH ABDOMINAL SEGMENT
Pretergite of abdominal segment 4 (=first gastral segment) subtended by a short narrow neck-like constriction. [Basicerotini: pretergite subsessile to sessile.]

BASIMANDIBULAR GLAND

Basimandibular gland present. [Basicerotini: basimandibular gland absent.]

This gland is variously developed in many genera of these two tribes (*Ishakidris, Microdaceton, Strumigenys, Glamyromyrmex*); it is universally absent from basicerotines. Its absence from some dacetonines (*Orectognathus, Acanthognathus*) may be secondary.

MESOPLEURAL GLAND

Anterolateral angle of mesopleuron bears a hair-filled glandular structure set in an emargination of the rim of the sclerite. [Basicerotini: mesopleural gland absent.]

This supposed gland varies from absent to massively hypertrophied in Dacetonini and Phalacromyrmecini. It is universally absent in Basicerotini.

Potential synapomorphies of Basicerotini + Phalacromyrmecini

BASE OF MANDIBLE

Base of mandible with a long stiff ventrally directed seta on ventral margin. [Dacetonini: such a seta absent.]

This specialised seta is present in all Basicerotini. In Phalacromyrmecini it is obvious in *Ishakidris*. Not recorded in the single specimen of *Phalacromyrmex* currently available, but this is in poor condition and badly mounted.

PROPODEAL SPIRACLE

Propodeal spiracle low on side of sclerite, abutting the margin of the small metapleural gland bulla. [Dacetonini: propodeal spiracle high on side, widely separated from metapleural gland.]

In the dacetonine genus *Acanthognathus* the spiracle abuts the metapleural gland bulla but here the spiracle is high on the side and the bulla is secondarily extended upwards.

Potential synapomorphies of Dacetonini + Basicerotini

None detected.

APPENDIX: Species dissected

The parts of all dissected specimens, whether partially or completely disarticulated, have been remounted on green-flagged card points and are deposited in The Natural History Museum, London. [List does not include the many taxa mounted with mandibles open and mouthparts displayed, but not otherwise dissected; these have been mounted on blue-flagged card points in the Natural History Museum, London, collection.]

Basicerotini

Basiceros: discigera, manni, militaris, singularis.

Eurhopalothrix: australis, biroi, bolaui, dubia, floridana, gravis, heliscata, insidiatrix, jennya, omnivaga, procera, punctata, speciosa, spectabilis, szentivanyi.

Octostruma: balzani, betschi, iheringi, inca, rugifera, stenognatha.

Protalaridris: armata.

Rhopalothrix: ciliata, isthmica, plus 1 unidentified species.

Dacetonini

Acanthognathus: brevicornis, ocellatus, rudis.

Codiomyrmex: thaxteri.

Colobostruma: alinodis, cerornata, plus 1 unidentified species.

Daceton: armigerum.

Epitritus: argiolus, hexamerus, laticeps, roomi.

Epopostruma: frosti.

Glamyromyrmex: beebei, excisa, flagellatus, semicomptus, sistrurus, tukultus, plus 2 unidentified species.

Gymnomyrmex: villiersi.

Kyidris: mutica, plus 1 unidentified species.

Mesostruma: browni, turneri.

Microdaceton: exornatum, tibialis, plus 1 unidentified species.

Neostruma: brevicornis, crassicornis, myllorhapha, zeteki.

Orectognathus: antennatus, clarki, mjobergi, szentivanyi, versicolor.

Pentastruma: sauteri.

Quadristruma: emmae.

Serrastruma: lujae, ludovici, serrula.

Smithistruma: alberti, angulata, dohertyi, fridericinuelleri, microthrix, ornata, transversa, truncatidens, plus 6 unidentified species.

Strumigenys: biolleyi, chyzeri, denticulata, doriae, elongata, gundlachi, godmani, koningsbergeri, louisianae, micretes, nidifex, pallestes, perplexa, precava, prospiciens, rogeri, rukha, saliens, signeae, subedentata, tigris, trieces, trudifera, plus 12 unidentified species.

Trichoscapa: membranifera.

Phalacromyrmecini

Phalacromyrmex: fugax.

Ishakidris: ascitaspis.

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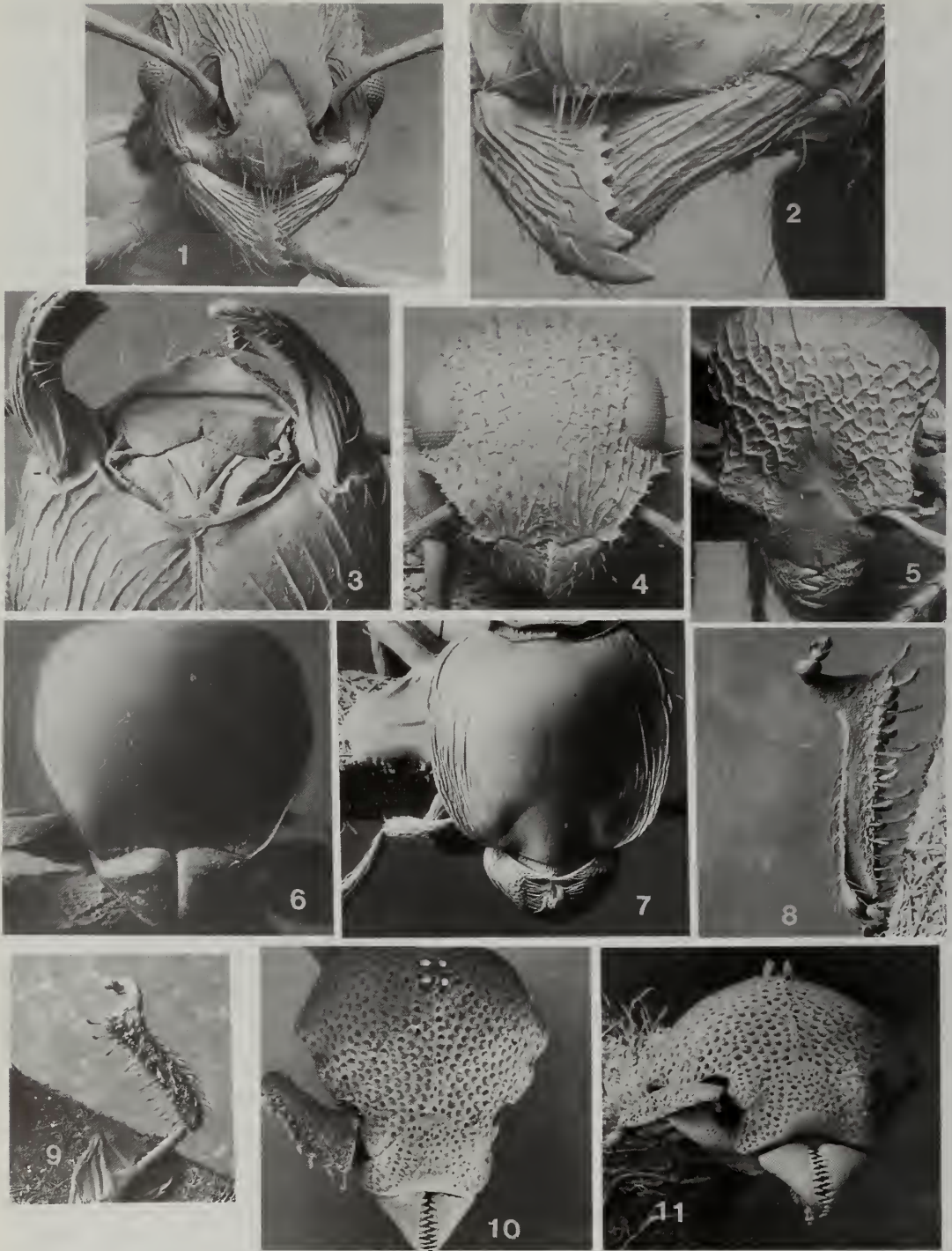
Figs. 1–11.   Worker ants: 1–3, Head of *Myrmica rubra*; 1, tilted slightly back from full-face view; 2, oblique close-up of fully closed mandibles; 3, ventral view to show buccal cavity; 4, head of *Cataulacus lujae*, tilted back from full-face view; 5–7, heads in full-face view of 5, *Pilotrochus besmerus*; 6, *Tatuidris tatusia*; 7, *Ishakidris ascitaspis*; 8–9, scape of *Basiceros singularis*, condyle uppermost; 8, ventral view; 9, dorsal view; 10–11, head of *Eurhopalothrix platisquama*; 10, full-face view; 11, oblique frontal view.

Figs. 12–22.   Worker ants: **12**, ventral head to show buccal cavity of *Eurhopalothrix platisquama*; **13–15**, heads in full-face view of 13, *Rhopalothrix ciliata*; **14**, *Protalaridris armata*; **15**, *Basiceros discigera*; **16**, oblique frontal view of head of *Basiceros singularis*, mouthparts extended and right mandible removed; **17**, occipital foramen of *Eurhopalothrix heliscata*; **18–19**, lateral view of head with antenna removed, of 18, *Basiceros singularis*; 19, *Eurhopalothrix platisquama*; **20**, frontal view of helcium of *Eurhopalothrix procera*; **21**, base of gaster in oblique ventral view of *Basiceros singularis*; **22**, head in full-face view of *Dysedrognathus* sp. n.

Figs. 23–33.   Worker ants. 23–25, head in full-face view of 23, *Smithistruma* sp. n.; 24, *Daceton armigerum*; 25, *Smithistruma reliquia*, mandibles open; 26–28, ventral view of head to show buccal cavity of 26, *Microdaceton* sp. n., mandibles open; 27, *Daceton armigerum*, right mandible and labio-maxillary complex removed; 28, *Smithistruma truncatidens*; 29–30, oblique frontal view of head to show labrum, mandibles removed, of 29, *Smithistruma truncatidens*; 30, *Strumigenys* sp. n.; 31, head in full-face view of *Smithistruma kerasma*, mandibles open; 32, head in ventrolateral view of *Colobostruma* sp.; 33, mandibles in oblique frontal view of *Microdaceton tibialis*.